MATE-GUARDING AND PATERNITY IN MANDRILLS (*MANDRILLUS SPHINX*): FACTORS INFLUENCING MONOPOLISATION OF FEMALES BY THE ALPHA MALE

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ABSTRACT

We use long-term data concerning mate-guarding and paternity in mandrills to (i) examine cycle-day and cycle selectivity by males; (ii) examine associations among male rank, peri-ovulatory mate-guarding, and paternity outcome; (iii) test the predictions of the priority-of-access model; and (iv) investigate factors influencing the ability of alpha males to monopolise females. Males mate-guarded peri-ovulatory days more than other receptive days, and conceptive cycles more than non-conceptive cycles. Both peri-ovulatory mate-guarding and paternity outcome correlated significantly with male rank. Alpha males accounted for 94% of peri-ovulatory mate-guarding and 69% of paternity, confirming the existence of extremely high reproductive skew in this highly sexually dimorphic species. The fit of the observed distributions of mate-guarding and paternity to predictions from the priority-of-access model was good, but in both cases the alpha males accounted for a greater proportion of reproduction than predicted. Mate-guarding was a good predictor of paternity, but consistently over-estimated the reproductive success of the alpha male. Splitting data into group-years revealed that % mate-guarding by the alpha male decreased with increasing numbers of adult males, while % paternity decreased with increasing numbers of reproductive males (all post-pubertal males). Further, mate-guarding became less effective as the number of reproductive males increased. We attribute this to the fact that only males aged 8+ yr mate-guarded, but that all males aged 3.8+ yr may sneak copulations, reducing the effectiveness of mate-guarding and therefore reducing paternity concentration in the alpha male.

KEYWORDS: dominance rank, priority of access, mating success, reproductive success

Where receptive females are aggregated in space, males can potentially defend access to them, favouring large, strong, competitive males that are capable of excluding less competitive rivals from mating (Darwin 1871). Thus, reproduction is expected to be skewed towards socially dominant males. In a review of the influence of dominance rank on a variety of measures of reproductive success, Ellis (1995) showed that, with the exception of primates, the available evidence upheld the hypothesis that dominant males should obtain greater reproductive success than do subordinate males. However, Ellis highlighted the fact that "most of the controversy surrounding whether or not dominance and RS [reproductive success] are positively related is confined to primates" (p. 259). Indeed, the influence of dominance rank on male reproductive success has long been a central issue in primate socio-biology (Altmann 1962; Carpenter 1942; Zuckerman 1932), and has been the source of a great deal of debate (Alberts et al. 2003; Bercovitch 1991; Bercovitch 1992; Bulger 1993; Cowlishaw & Dunbar 1991; van Noordwijk & van Schaik 2004). In general, high-ranking males do sire more offspring than low-ranking males. However, variation in the relationship between dominance rank and male reproductive success has been demonstrated at the species, population and group level, and at the temporal level within the same group (see van Noordwijk & van Schaik 2004 for a recent review).

The strength of the relationships among male rank, mating success and paternity, and the resulting degree of reproductive skew in favour of alpha males, can be expected to depend on a number of factors that influence the ability of high-ranking males to monopolise access to receptive females. These include the number of females available and the temporal distribution of female receptivity (Emlen & Oring 1977; Ims 1989; Shuster & Wade 2003); the number of rival males present and the success of alternative mating strategies by subordinate males; male mate choice where females differ in quality or likelihood of conception; female reproductive strategies including mate choice (Alberts et al. 2003; Bercovitch 1991) and strategies to increase the number of males mated with (Hrdy 1979; van Schaik et al. 2004); and interactions between male and female strategies (e.g. Soltis et al. 2001).

A larger female cohort size increases the chances of females cycling synchronously, posing a

problem for the top-ranking male. In such cases, the priority-of-access model predicts that dominance rank should function as a queue for mating opportunities (Altmann 1962; Hausfater 1975; Suarez & Ackerman 1971). Males of any given rank are not expected to mate-guard unless all higher-ranking males are already mate-guarding. Where females are asynchronously receptive, the top-ranking male should monopolise reproduction, but where more than one female is simultaneously receptive males of lower ranks are also expected to mate-guard. Variability in male mating and reproductive success thus should directly reflect male dominance status and the number of simultaneously oestrous females (Altmann et al. 1996).

Even when female receptive periods are asynchronous, an increased number of receptive females may reduce alpha male monopoly of receptive females, as the costs associated with mate-guarding (risks of conflict with rival males and constraints on foraging, Alberts et al. 1996; Bercovitch 1983) may render an alpha male unable to guard successive females continuously, or almost continuously, over long periods. For example male chacma baboons mate-guard for only 9-12 days per month, regardless of the availability of peri-ovulatory females, and leave some peri-ovulatory females un-guarded, implying that males are able to afford the costs of mate-guarding for a limited period only (Weingrill et al. 2003).

Increased numbers of males (residents and extra-group males) are predicted to reduce monopoly of receptive females by high-ranking males for three reasons. First, increased numbers of rival males imply that more subordinate males are available to employ alternative strategies, including surreptitious matings (Setchell in press) that act to reduce the effectiveness of mate-guarding and more potential partners for coalition formation to displace mate-guarding males (Bercovitch 1988; Noë & Sluijter 1990; Watts 1998). Second, the presence of many males may result in decreased power differentials between individual males, making it more difficult for the alpha male to monopolise females. Even males with high resource-holding potential may be “swamped”, and unable to resist repeated challenges from multiple rivals (Cowlishaw & Dunbar 1991). Finally, the presence of more rivals may also make the male dominance hierarchy less stable, and rank instability itself may also weaken the relationship between male rank and reproductive success (Cowlishaw & Dunbar 1991).

Finally, models of dominance-based priority-of-access to receptive females assume that all female cycles are equal. However, this is unlikely to be the case, and males may be expected to apportion costly mating effort in relation to the quality of an individual female and cycle. In particular, males are expected to mate-guard on days when females are most likely to be fertile, in preference to other days, and should mate-guard conceptive cycles in preference to non-conceptive cycles, if they are able to distinguish between the two (e.g. Bulger 1993; Weingrill et al. 2003).

Due to the difficulty of collecting long-term data for long-lived, slow-reproducing species, few studies have examined temporal variation in the extent to which male rank predicts male reproductive success in primates (but see Alberts et al. 2003; Widdig et al. 2004). The predictions of the priority-of-access model have only been tested in detail for baboons (Alberts et al. 2003; Altmann et al. 1996; Bulger 1993; Hausfater 1975; Noë & Sluijter 1990; Weingrill et al. 2000), although Soltis et al. (2001) has shown that the number of females mating simultaneously is associated with the strength of the correlation between male dominance rank and reproductive success in Japanese macaques (*Macaca fuscata*), and breeding seasonality (an estimator of female cycle synchrony) is known to influence the association between male rank and reproductive success (Paul 1997; van Noordwijk & van Schaik 2004). Tests of the priority-of-access model in baboons have revealed interesting sub-species differences. In chacma baboons (*Papio cynocephalus ursinus*) male mating success shows a very close fit to a dominance-based priority-of-access model (Bulger 1993; Weingrill et al. 2000). In yellow baboons, however, although the correlation between observed mating behaviour and paternity and that expected from priority-of-access model can be high (Altmann et al. 1996), the quantitative fit to the priority-of-access model is generally poor (Alberts et al. 2003). Alberts et al. (2003) attribute these sub-species differences to the expression of male-male coalitionary behaviour in yellow baboons, a behaviour which has not been observed for chacma baboons.

In this study we investigate the relationships among male rank, mating success and paternity outcome in a semi-free-ranging colony of mandrills, using 13 group-years of behavioural observations and ten group-years of paternity results. Mandrills were formerly thought to be close relatives of *Papio* baboons, but are in fact more closely related to *Cercocebus* mangabeys (Disotell et al. 1992; Fleagle & McGraw 1999). They are one of the most sexually dimorphic primate species, suggesting that male-

male competition for access to peri-ovulatory females is intense. Adult males (31 kg) are 3.4 times the mass of females (Setchell et al. 2001), have upper canines measuring 44 mm (Setchell & Dixson 2002), and possess showy secondary sexual ornamentation, including brightly coloured skin on the face, rump and genitalia.

Mandrills are found only in the dense rainforest of central Africa (Gabon, Republic of Congo, Equatorial Guinea and Cameroon, Grubb 1973), and have so far proved impossible to habituate in the wild. Most of our knowledge of reproduction in this species therefore comes from a semi-free-ranging colony of animals at the Centre International de Recherches Médicales, Franceville (CIRMF), Gabon. Studies of this colony show that multiple males associate with the social group of females and their young (Setchell & Dixson 2001a; Wickings et al. 1993), and observations from the wild confirm this multi-male, multi-female social system (Abernethy et al. 2002). Breeding is moderately seasonal, with the majority of female receptive periods occurring between June and October (Setchell & Wickings 2004).

DNA analyses have shown that the alpha male mandrill sires the majority of offspring in a mating season (Charpentier et al. 2005; Dixson et al. 1993; Wickings 1995; Wickings et al. 1993). However, the only available behavioural data regarding reproduction concern 12 conceptive cycles during a single mating season (Dixson et al. 1993; Wickings et al. 1993). Like chacma baboons, male mandrills do not form coalitions (Setchell & Wickings 2005), predicting that mandrills should fit the priority-of-access model. If, however, lower-ranking males still manage to sire more infants than expected, then sneak copulations are the most likely explanation, in view of the dense forest habitat.

Objectives of this study were (i) to examine patterns of mate-guarding by cycle-day, as this is the first detailed study of mate-guarding in mandrills, and to compare conceptive and non-conceptive cycles; (ii) to examine the relationships among male rank, peri-ovulatory mate-guarding and paternity outcome; (iii) to examine specifically the predictions of the priority-of-access model; (iv) to investigate variation in alpha male monopoly of mating and reproduction, and inconsistencies between mate-guarding and paternity outcome, in relation to numbers of receptive females, numbers of adult and reproductive males, and alpha male tenure.

METHODS

Study Animals

The CIRMF mandrill colony was established in 1983/4, when 15 animals (7 males, 8 females) were released into a 6.5 ha forest enclosure (E1). There have been no subsequent additions to the colony, other than by breeding, although animals have occasionally been removed, and in 1994 a second semi-free-ranging group was established in a smaller enclosure (E2, 3.5 ha) by transferring 17 mandrills (including 6 adult females and 4 adult males) from the first enclosure. The animals forage freely and receive daily supplements of monkey chow, fruit and vegetables. Water is always available from a stream, which runs through both enclosures. Behavioural observations are made twice daily (approx. 10h00-11h30 and 15h30-17h30) from a tower overlooking the enclosures. This study makes use of records of female cycle status and male mate-guarding for E1 and E2 for the eight year period 1996-2003. The size and age-sex composition of the study groups during this period is shown in Table 1, and corresponds to the smaller groups observed in the wild (Rogers et al. 1996).

All males above the age of 3.8 yr, the age at which the testes descend (Setchell & Dixson 2002), were considered potentially reproductive. However, males do not attain adult body mass, crown-rump length or full expression of secondary sexual traits until 10 yr (Setchell & Dixson 2002). Males aged 3.8-8.0 yr (sexually mature, but small) were termed young adolescent males, males aged 8.0-10.0 yr (sexually mature, approaching adult size and appearance) were termed older adolescent males, and males aged 10.0 yr and older (full size) were termed adult males. Females were termed reproductive once they had shown their first full swelling cycle (see below), nulliparous when they had not yet given birth to an infant, and parous when they had already given birth.

Female Cycle Status

Female mandrills show sexual swellings that increase in size during the follicular phase, reaching maximum size around the time of ovulation. No endocrine data are yet available for

mandrills, but studies of closely related baboons have shown that increase in sexual swelling size co-occurs with increased estrogen levels during the follicular phase of the menstrual cycle; a rapid decrease in sexual swelling size (break-down) coincides with a post-ovulatory rise in progesterone; and the swelling detumesces during the luteal phase until it is flat (Shaikh et al. 1982; Wildt et al. 1977). Cycle days were numbered according to the day of deflation, with the day of break-down termed day 0, and preceding days assigned negative numbers (following Hausfater 1975). We restricted analyses of male mating success to the six days before swelling break-down, termed the "peri-ovulatory period". This encompasses the period during which ovulation and conception are most likely to occur (Hendrickx & Kraemer 1969; Shaikh et al. 1982; Wildt et al. 1977). Cycles were termed conceptive when they preceded the appearance of a pregnancy swelling. All such cycles during the study period resulted in the birth of a live, full-term infant.

Mate-Guarding

Systematic, focal observations of sexually receptive females are not possible under colony conditions. We therefore used the occurrence of mate-guarding as a behavioural estimate of male attempts to secure unique access to a receptive female. This is an easily observed, unambiguous behaviour, where a male maintains close spatial proximity to a female, and monitors her continuously, and has commonly been used as a measure of mating success in baboons (Alberts et al. 2003; Altmann et al. 1996; Bercovitch 1986; Bulger 1993; Noë & Sluijter 1990; Smuts 1985; Weingrill et al. 2000).

Daily records were kept of the occurrence of mate-guarding, with the identity of the male and female involved, and the reproductive status of the female. Mate-guarding dyads were not observed to change between morning and afternoon observation sessions. This observation was reinforced by *ad libitum* observations at other times, which also suggested that mate-guarding males remained in close proximity to the females at night, although darkness presumably increases the chances of sneak copulations. We therefore assumed that mate-guarding continued outside observation periods. Cycles for which observations were available for fewer than four of the six peri-ovulatory days were discarded from behavioural analyses. Observations were available for four or more peri-ovulatory days for 171

female cycles, from 44 females (mean±sem 3.9±0.5 cycles per female, range 1-16, distribution across the years of the study is shown in Table 1).

Dominance Hierarchies

Rank relations between males were determined using *ad libitum* records of avoidance behaviour during daily observation periods. With the exception of occasional dramatic changes in male rank, that occurred from one day to the next and usually involved a change in alpha male (see Results), all adult and older adolescent males could be assigned a rank for each mating season, although data were not always available for younger adolescent males. We should note that our focus on the influence of male rank means that the same male may contribute to data for multiple ranks over the study period.

Paternity Determination

Paternities were determined for 74 of the 91 offspring (81%) born following mating seasons in 1996-2001 (insufficient or no blood samples were available for the remaining 17 individuals). The distribution of known paternities by group and mating season is shown in Table 1. Details of paternity determination can be found in Charpentier et al. (2005). Briefly, DNA was extracted from blood samples obtained during annual captures. Maternity was verified and paternity assigned using eight to ten microsatellite loci. Genotypes were available for all potential sires (all reproductive males present at the time of conception), and paternity was assigned using CERVUS 2.0 (http://helios.bto.ed.ac.uk/evolgen/cervus). CERVUS 2.0 is based on the likelihood-based approach described in Marshall et al. (1998). Simulations were carried out to estimate the critical difference in log-likelihood score between the most likely and the second most likely candidate father. Simulation input parameters were 2.4% rate of typing errors, 92.6% of loci typed and 10 000 cycles, with 100% of candidate males genotyped. In 65 cases CERVUS assigned a sire with a 95% confidence level, and for a further nine cases CERVUS sires were attributed at only a relaxed level (80%). In the latter cases, PARENTE (Cercueil et al. 2002) was used to confirm the sire. This software uses a Bayesian method to calculate the probability of paternity for each sire using information from all possible sires in

the population. For each individual, PARENTE verifies the genetic and age compatibilities for all potential triads (individual, potential mother, potential father), and calculates the probability that a parentage link is correct using the allelic frequencies and the sampling rate of the population, taking into account incompatibilities and the error rate (estimates of the error rate in the data and mean proportion of loci typed were the same as for CERVUS).

Data Analysis

Analyses of peri-ovulatory mate-guarding were conducted using (i) data for all cycles for which data were available, (ii) conceptive cycles only, and (iii) separately for each of the 13 group-years for which data were available (1996-2003, no data for either enclosure in 1999, none for E2 in 2001). Mating success for each individual male was defined as the number of peri-ovulatory days that he mate-guarded. Mating success for each male rank was defined as the number of peri-ovulatory days on which a male of that rank was observed to mate-guard.

Analyses of reproductive success were conducted for the period 1996-2001, and separately for each of the ten group-years for which data were available (1996-2001, no data for either enclosure in 1999 because no females conceived). Reproductive success for each individual male was defined as the number of offspring sired, and reproductive success for each male rank was defined as the number of offspring sired by a male of that rank.

Factors influencing monopoly by the alpha male

The ability of the alpha male to monopolise receptive females was investigated using the % of all peri-ovulatory mate-guarding performed by the alpha male for each group-year. All cycles (conceptive and non-conceptive) were used in this analysis, as we could not assume that non-conceptive cycles were non-fertile. The ability of the alpha male to monopolise reproduction was investigated as the % offspring of known paternity that he sired. We chose to examine % monopoly by the alpha male (similar to the "paternity concentration" variable used by van Noordwijk & van Schaik 2004), rather than the correlation coefficient between male rank and reproductive success (e.g.

Cowlishaw & Dunbar 1991), due to the high numbers of non-sires in each year, the small cohorts of reproductive males in some years, and the problematic influence of younger adolescent males on correlation coefficients (Bercovitch 1986; McMillan 1989).

Predictions of the priority-of-access model

The priority-of-access model predicts that lower-ranking males should mate-guard females only on days when more than one female is simultaneously peri-ovulatory. The expected distribution of mate-guarding amongst males was therefore calculated from the observed overlap of female peri-ovulatory periods during the study period as follows: the expected proportion of mate-guarding by the alpha male equalled the number of days that one or more female was peri-ovulatory, divided by the total number of female days; the expected proportion of mate-guarding by the second male equalled the number of days that two or more females were peri-ovulatory, divided by the total number of female days; and so on for lower-ranking males. Both conceptive and non- conceptive peri-ovulatory periods were used in this analysis, as we had no way of knowing whether non-conceptive cycles were fertile or not.

Priority-of-access predictions for paternity were calculated using only conceptive peri-ovulatory periods for which the sire of the resulting offspring was known, and based on the maximum number of females overlapping on any one day of the peri-ovulatory period concerned. Thus where no other female was simultaneously peri-ovulatory, the alpha male was awarded the offspring. Where one other female was simultaneously peri-ovulatory, the alpha was awarded 1/2 an offspring, and the second-ranking male 1/2 an offspring. Where two other peri-ovulatory females were also available on any one day of the peri-ovulatory period, the alpha was awarded 1/3 of an offspring, the second-ranking male 1/3 of an offspring, and the third male 1/3 of an offspring, etc. These predictions are conservative, as they assume that a female is equally likely to conceive on each of the six days of the peri-ovulatory period. If, in reality, males can determine likelihood of ovulation more precisely, then they will not need to mate-guard all six days of the peri-ovulatory period.

Deviation from the priority-of-access model

To examine factors influencing the fit of the priority-of-access model to the observed data, deviation of the observed proportion of all mate-guarding attributed to the alpha male from the expected proportion of all mate-guarding by the alpha male was calculated for each group-year as % observed less % expected, divided by % expected, using expected values calculated using the priority-of-access model. A similar variable was calculated for deviation of observed paternity from the priority-of-access model.

Potential influences on alpha male monopoly of reproduction

To determine the best predictor(s) of the extent of alpha male monopoly of mate-guarding and paternity, the number of males siring per year, deviation from the priority-of-access model for mate-guarding and paternity, and the discrepancy between alpha male mate-guarding and paternity, we used stepwise multiple linear regression with a forward selection procedure, and the following independent variables: numbers of receptive females, adult males and reproductive males (adults and adolescents) present in the group, and the tenure of alpha male (P to enter = 0.05, P to remove = 0.10). All variables were normally distributed (skew / standard error of skew <3, Zar 1996). Although variables which contribute to total group size (numbers of receptive females, adult males and reproductive males) are clearly related, in no case was tolerance <0.336 (VIF>2.97), meaning that collinearity was not a serious problem in these analyses (Quinn & Keough 2002 propose tolerance <0.1, or VIF>10.0, as an approximate guide to unacceptable collinearity).

All statistical analyses were performed using SPSS 11.0. Means are quoted as mean±SEM.

RESULTS

Male Dominance

Patterns of male avoidance revealed that there was always one top-ranking male (alpha male) in a group. All other males avoided this individual, who never avoided other males. Of a total of 20

males (12 in E1, 8 in E2) that were already adult at the beginning of the study, or who reached adulthood during the study period, nine attained top-rank (seven in E1, two in E2). Males attained top-rank at age 8.8-12.6 yr (mean 10.8±0.6), and lost top-rank at 10.5-19.0 yr (mean 13.8±1.3 yr).

Six changes in alpha male occurred in E1 during the eight-year study period. All five of these that occurred naturally (i.e. were not as a result of human intervention) occurred when at least one female (and up to 10 females) showed sexual swellings. In three of the four cases where details of the take-over were known, two or more females were peri-ovulatory. Mean male tenure in this enclosure was 1.6±0.5 yr (range 0.2-3.5 yr). By contrast, only one change in alpha male occurred in E2 during the study. One female showed a sexual swelling at the time of the take-over, but none were peri-ovulatory. The tenures of the two alpha males in this enclosure were 2.4 yrs (estimated date of take-over) and a minimum of 7.5 yrs (on-going at the end of the study) respectively. Differences in group size may help to explain the difference in alpha male turnover and tenure between the two enclosures. First, E1 contained significantly more reproductive females per year across the study period than E2 (Table 1, $t_{12}=3.12$, $p=0.009$). Second, fewer males matured and reached adulthood in E2 (4 maturing males, mean 0.6±0.6 per year) than in E1 (11 maturing males, mean 1.4±1.0 per year), although this difference was not significant ($t_{12}=0.81$, $p=0.096$).

Mate-Guarding

Cycle-day selectivity

Timing of mate-guarding relative to day of break-down was similar for both conceptive and non-conceptive cycles (**Fig. 1**). Mate-guarding never occurred earlier than day –25 (although females could show sexual swellings from up to day –40), after the day of break-down, or during pregnancy. Mate-guarding increased gradually from day –24, remaining less than 20% until day –10. It was highest during the presumed peri-ovulatory period (days –6 to –1), peaking on day –4 (conceptive cycles) and –3 (non-conceptive cycles), and decreasing abruptly to less than 1% on the day of break-down. The maximum percentage of females mate-guarded on any one cycle day was 57% (conceptive cycles) or 51% (non-conceptive cycles). Mate-guarding during conceptive cycles was

systematically higher than during non-conceptive cycles after day –19 (paired t-test for days –20 onwards: t_{20}=4.89, p<0.001).

Alpha males mate-guarded with the highest frequency on all cycle days for both conceptive and non-conceptive cycles, while non-alpha males never mate-guarded more than 5% of days observed for any cycle day (mean 1.6±0.3%, day –20 to break-down). The marked increase in mate-guarding towards and during the peri-ovulatory period was thus due almost entirely to increased mate-guarding by the alpha male. Plotting mate-guarding vs. days since swelling onset revealed no marked peak in male sexual activity (**Fig. 1**).

Cycle selectivity

Where alpha males (who had "free" choice) had the choice of two females, one of which conceived and the other did not, they were significantly more likely to mate-guard the female that conceived (n=34) than the female that did not conceive (n=11, X^2_1=11.76, p<0.001). Where three peri-ovulatory females were available simultaneously, but only one of the three conceived, the alpha male mate-guarded the female that conceived on 10 occasions, and mate-guarded one of the other two females on eight occasions. This was significantly different from random choice, which predicts that the male should guard the female that conceived on 1/3 of days (X^2_1=4.00, p=0.046). Finally, where two of the three available females conceived (n=10 cases), the alpha male mate-guarded one of these two females on 9 occasions, and the female that did not conceive on only 1 occasion, although this was not significantly different from random choice (X^2_1=0.245, p=0.118).

Who mate-guarded?

Most female cycles were mate-guarded by only one male, with a maximum of three males mate-guarding during any one cycle or peri-ovulatory period, and a maximum of two males mate-guarding during any conceptive peri-ovulatory period (**Fig 2**). Seventeen males mate-guarded at least once during the study period, but only eleven of these mate-guarded during a conceptive peri-ovulatory period. Mate-guarding males were aged 8.3-18.8 yr, with a mean age of 12.8±0.5 yr (using

one age-point for each mate-guarding male per mating season). Variance in total days mate-guarded was high among males that mate-guarded at least once. The most successful male in E1 accounted for 33% of all conceptive peri-ovulatory mate-guarding, while the most successful male in E2 accounted for 83%, a difference related to the difference in alpha male tenure in the two groups. The individual contribution of mate-guarding males ranged from 1-121 conceptive cycle days (mean 29±10 days), 0-48 non-conceptive cycle days (mean 13±4 days), 0-83 conceptive peri-ovulatory days (18±6 days), and 0-40 non-conceptive peri-ovulatory days (9±3 days). Of the 26 males that attained the age of 8 yr prior to or during the study period, nine (35%) were never observed to mate-guard.

Continuous mate-guarding

The distribution of female cycles was such that alpha males often mate-guarded one female immediately after another. Unbroken data (with no missing days) were only available for portions of the study period, limiting investigation of continuous mate-guarding. However, data from the most complete years (1996 and 1997) showed that alpha males mate-guarded individual females continuously for a mean of 5.3±5.4 days, and the alpha male could mate-guard continuously for up to 22 days (with the same or multiple females), and for much longer periods with only 1-3 days without mate-guarding (e.g. 58 days in 1996).

Relationship between male dominance rank and mate-guarding

Males ranked 1-3 mate-guarded during conceptive peri-ovulatory periods, while males ranked 1-4 mate-guarded during non-conceptive peri-ovulatory periods. Males ranked 1-6 mate-guarded on other cycle days (conceptive and non-conceptive), but males ranked 6+ never mate-guarded. Alpha males accounted for over 90% of mate-guarding and where a change in alpha male occurred, the new alpha male took over mate-guarding on the same day that he took over top-rank.

The number of peri-ovulatory days (conceptive and non-conceptive) mate-guarded and male rank were highly and significantly correlated (lumping males ranked 6+ because they did not mate-guard: r_S=-0.899, p=0.015, n=6, the correlation is negative because the top-ranked male ranks 1, **Fig.**

3), and this remained the case when the alpha male was removed from analysis (r_s=-0.900, p=0.037, n=5). The number of males available to mate-guard (i.e. those aged 8+ yr) during a mating season ranged from 4-11, and potentially mate-guarding males ranked 5 and 6 were not available for two of the 13 group years. However, correcting the proportion of mate-guarding due to each rank for opportunity (the number of peri-ovulatory days available to males of that rank aged 8+ yr and therefore available to mate-guard) only increased the strength of the correlation between dominance rank and peri-ovulatory days mate-guarded (r_s=-0.943, p=0.005, n=6).

Using only mate-guarding during conceptive peri-ovulatory periods, alpha males accounted for 94% of mate-guarding (258/275 days), second-ranking males for 2% (6 days) and third-ranking males for 4% (11 days). Here the correlation with rank, lumping all ranks that did not mate-guard, was non-significant (r_s=0.400, p=0.600, n=4). However, including all males aged 8+ yr (i.e. males available to mate-guard) resulted in a significant negative correlation with male rank (r_s=-0.880, p=0.021, n=6). As there were always more than three males aged 8+ yr present, it was not necessary to adjust these figures for opportunity.

Factors influencing monopoly of mate-guarding by the alpha male

The alpha male accounted for 77-100% of peri-ovulatory mate-guarding (mean 94±2%) in any one group-year, and was the only male to mate-guard peri-ovulatory females for seven of 13 group-years. The number of males that mate-guarded during any one group-year ranged from 1-4 (mean 2.0±0.3), representing 11-80% (mean 32±6%) of the males aged 8+ yrs available to mate-guard. The only significant predictor of alpha male monopoly of mate-guarding was the number of adult males present, while the number of reproductive males, number of receptive females and alpha male tenure were excluded from the model (Table 2). The alpha male monopolised all mate-guarding until there were more than three adult males present, and was capable of doing so until more than 5 adult males were present.

Mate-guarding and the priority-of-access model

Although up to 16 females could show sexual swellings on any one day, a maximum of six were simultaneously peri-ovulatory, and on 65% of peri-ovulatory days no other female was peri-ovulatory (**Fig. 4**). There were more adult males present than there were peri-ovulatory females for all but 12 of 889 peri-ovulatory days (1%), and there were always more males aged 8+ yrs available than peri-ovulatory females (i.e. the operational sex ratio was always male biased). However, only one male mate-guarded on 381 of 403 mate-guarded peri-ovulatory days (95%), and a maximum of two males mate-guarded on any one peri-ovulatory day (22 days).

Figure 3 includes the predicted proportion of mate-guarding for males of each rank, calculated using the priority-of-access model, for all peri-ovulatory days for which mate-guarding information was available. The predicted number of mate-guarding days are greater than the observed figures, because mate-guarding occurred on only 403 of 948 (43%) of available peri-ovulatory days (see also Fig. 1). The qualitative match between the observed and predicted distributions of mate-guarding by rank was good, but not perfect, and deviation from the model was significant (X^2_3=28.47, p<0.001). This was due to the alpha male mate-guarding proportionally more than expected (observed 90%, expected 73%), the second- and third-ranking males mate-guarding proportionally less than expected (rank 2: observed 5%, expected 21%; rank 3: observed 3%, expected 5%), and males ranked 5 and 6 mate-guarding, although they were not expected to do so.

Deviation of observed mate-guarding from the priority-of-access model

The expected proportion of all mate-guarding that was accounted for by the alpha male, predicted from the priority-of-access model, ranged from 63-100% across the 13 group years, with a mean of 83±3%. With one exception, where the alpha male mate-guarded less than expected, observed mate-guarding by the alpha male was consistently higher than predicted (mean deviation from the expected value 0.15±0.04, range –0.20-0.38). The only significant predictor of deviation from expected mate-guarding was the number of receptive females present, while the number of adult males, number of reproductive males, and alpha male tenure, were excluded from the model (Table 2). As the number of receptive females increased, deviation from the priority-of-access model also increased (alpha males mate-guarded more than expected).

Paternity Outcome

Fourteen males sired offspring (ten in E1, four in E2) during the ten group-years for which both paternity and mate-guarding data were available, although only six males mate-guarded conceptive peri-ovulatory females during this period (4 in E1, 2 in E 2). Sires were aged 5.6-18.7 yr, with a mean age of 11.4±0.6 yr (n=29, using the age mid-point for each sire per mating season). Variance in number of offspring sired was high (E1: 1-13 offspring, mean 5.1±1.4 offspring, E2: 1-18 offspring, mean 5.8±4.1 offspring). The most successful male in E1 sired 25% of offspring, while the most successful male in E2 sired 78% of offspring in their respective groups (due to differences in alpha male tenure between the two groups).

Relationship between male dominance rank and paternity outcome

Alpha males sired 51 of 74 offspring (69%), while the remaining 31% were sired by males ranked 2-10, with non-alpha males at each rank siring a maximum of five offspring (7%) (**Fig. 5**). The mean rank of sires was 1.9±0.2 (median 1, range 1-10), while the mean rank of the 23 non-alpha sires was 3.7±0.5 (median 3, range 2-10). Contribution to paternity was significantly correlated with male dominance rank (lumping ranks greater than 10, r_s=-0.837, p=0.003, n=10). This was not only due to the influence of alpha males, as the correlation remained significant when they were removed from analysis (r_s=-0.760, p=0.018, n=9). The number of offspring sired by males of each rank should be corrected for opportunity, as there were not always 10 potential sires available. However, a minimum of 8 potential sires was always available (Table 1), and lumping ranks 8+ did not change the significance of the result (r_s=-0.898, p=0.002, n=8).

Factors influencing monopoly of paternity by the alpha male

Alpha males sired more offspring than any other male in all group-years. The % paternity due to the alpha male ranged from 33-100% (mean 74±6%, 10 group-years), while the number of males siring ranged from 1-5 (mean 2.9±0.5) or 10-33% (mean 23±3%) of reproductive males available. The

only significant predictor of both % paternity by the alpha male and the number of males siring was the number of reproductive males in the group, while the number of receptive females, number of adult males, and alpha male tenure were excluded from both models (Table 2). As the number of reproductive males present increased, % paternity by the alpha male decreased, and the number of sires increased.

Paternity outcome and the priority-of-access model

Fig. 5 includes predictions for paternity based on the priority-of-access model. The observed distribution of paternity was not significantly different to that predicted (lumping males ranked 4+, due to low expected counts: X^2_3=7.48, p=0.058). However, alpha males exceeded their predicted reproductive success by 1.2 times, while second and third-ranking males sired fewer offspring than predicted (44% and 62% of offspring predicted). Notably, seventh and tenth ranking males were predicted not to sire at all, whereas they sired three offspring.

Deviation of observed reproductive success from the priority-of-access model

The value of the deviation from predictions of the priority-of-access model (whether the alpha sired more or fewer offspring than predicted) ranged from –0.20 to 0.63 (mean±sem 0.11±0.08, n=10 group-years), and the alpha sired more offspring than predicted in eight of ten group-years. However, none of the variables tested (numbers of cycling females, adult males, reproductive males, and alpha male tenure) significantly predicted this measure of deviation.

Relationship between mate-guarding and paternity outcome

At a general level, the number of offspring sired by a male was significantly positively correlated with both the number of days that he mate-guarded conceptive peri-ovulatory females (r_s=0.636, p=0.019, n=13 sires, **Fig. 6**), and the number of conceptive cycles that he mate-guarded (r_s=0.648, p=0.017, n=13, both analyses based only on the period for which paternity data were available). This was also the case when only the six mate-guarding males were considered (number of

days: r_s=0.812, p=0.050; number of cycles: r_s=0.928, p=0.008).

At the level of individual offspring, of 57 infants where observations were available for the peri-ovulatory period of the conceptive cycle the alpha male sired 37 (79%). The alpha male was significantly more likely to sire the resulting offspring if he mate-guarded during the peri-ovulatory period than if he did not (X^2_1=3.96, p=0.046). Further, the alpha male mate-guarded more (median 50% of peri-ovulatory days) when he sired the resulting offspring than when he did not (median 20%, U=254.00, z=1.96, p=0.050), although the range for both conditions was 0-100%, meaning that even where the alpha male mate-guarded during the entire peri-ovulatory period, he was not necessarily the sire. In only one case (5%) did a non-alpha male both mate-guard and sire the resulting offspring. All males that mate-guarded sired offspring, but the six males that did not mate-guard sired 20 of 74 offspring (27%), indicating the success of surreptitious mating tactics.

Factors influencing the discrepancy between mate-guarding and paternity

Although alpha males dominated both mate-guarding and paternity, behavioural mating success over-estimated reproductive success by the alpha male. The % offspring sired by the alpha male in any one group-year was lower than % peri-ovulatory mate-guarding by the alpha male (Wilcoxon matched-pairs test: Z=2.52, p=0.012, n=10 group-years), and more males sired (1-5) than mate-guarded (1-3) during any one year (Z=2.91, p=0.004, n=10). The discrepancy between % mate-guarding and % paternity by the alpha ranged from 0-55% (mean 21$\pm$5%). The only significant predictor of this discrepancy was the number of reproductive males present in a group, while the number of adult males, number of receptive females, and alpha male tenure were excluded from the model (Table 2). As the number of reproductive males increased, the discrepancy between mate-guarding and paternity by the alpha male also increased.

DISCUSSION

The results presented here confirm a robust relationship between rank and reproduction in mandrills, with alpha males dominating both mate-guarding and paternity. However, the strong control that alpha

males exert over receptive females (in the form of mate-guarding) does not necessarily translate into the proportion of offspring sired. This appears to be due to alternative reproductive tactics by other males, in the form of sneak copulations, reducing the effectiveness of mate-guarding. As the number of rival adult males increased, the proportion of mate-guarding by the alpha male decreased. As the number of rival reproductive males (of all ages) increased, the proportion of paternity attributed to the alpha male decreased, the number of males siring increased, and the effectiveness of alpha male mate-guarding decreased (the discrepancy between % mate-guarding and % paternity by the alpha male increases). As for male rhesus macaques (Widdig et al. 2004), yellow baboons (Alberts et al. 2003), blue monkeys (*Cercopithecus mitis*, Cords 2000), domestic cats (*Felis catus*, Say et al. 2001), and spotted hyaenas (*Crocuta crocuta*, Engh et al. 2002), these data for mandrills provide more support for limited or incomplete control models of reproductive skew, which predict that subordinates will reproduce when the capacity of dominant individuals to monopolise reproduction is reduced (Cant 1998; Clutton-Brock 1998; Reeve et al. 1998), than for concession models, which propose that dominant individuals have full control of reproduction, but allow subordinates to reproduce where such reproduction brings benefits to dominants, for example by enticing subordinates to remain and help to defend the group (e.g. Johnstone et al. 1999; Vehrencamp 1983).

Monopolisation of females and consequent paternity concentration in the alpha male leads to very high short-term variance in male reproductive skew. Whether this variance is maintained over a longer time-scale depends on the length of alpha male tenure, and whether all males attain alpha status at some stage during their career. Alpha male tenure was shorter where the number of maturing rivals and the number of females were higher. Similarly, Alberts et al (2003) found that the tenure of alpha male yellow baboons was predicted most strongly by the number of adult males present, although the variance explained was low. Thus larger groups not only reduce reproductive skew by reducing the ability of the alpha male to monopolise females, but also by reducing the tenure of alpha males, meaning that more males attain high status and reproductive success, but for shorter periods, and decreasing variance in male lifetime reproductive success. However, examination of male careers shows that not all males attain alpha status during their lifetime in this colony and variance in male life-time reproductive output is high, and higher than in females, in agreement with the large body size, well developed weaponry and late age at maturity in males when compared to

females (Setchell et al. 2005).

Cycle-day and Cycle Selectivity

As reported for other primate species (reviewed by Dixson 1998), male mandrills showed clear preference for the peri-ovulatory period of the female cycle. Our finding that males only mate-guarded 43% of peri-ovulatory days is likely due to the error associated with a six-day peri-ovulatory period estimate. If alpha males are able to predict the fertile period of a female more accurately than this six-day window, then they need not necessarily mate-guard higher-ranking females on each day of their peri-ovulatory period, but only on days when conception is likely. Cycle day selectivity was not related to the day of onset of sexual swelling, implying that the peri-ovulatory period could not be predicted from the duration of sexual swelling. As suggested for other species with sexual swellings (e.g. Weingrill et al. 2003), it seems that male mandrills may rely on additional cues to determine timing of female ovulation, including olfactory (ano-genital secretions) and tactile (swelling turgidity) cues, as well as visual inspection of swellings.

Males also appeared to be able to distinguish females that conceived from those that did not, mate-guarding the former more than the latter. However, it is not possible to distinguish between cause and effect here, and the possibility remains that females are more likely to conceive when they receive more mate-guarding. Male ability to distinguish fertile cycles from non-fertile swellings has also been reported for chacma baboons (Bulger 1993; Weingrill et al. 2003), and sooty mangabeys (*Cercocebus torquatus atys*), where males are able distinguish fertile swellings from post-conception swellings, although these are visually the same (Gordon et al. 1991; Gust 1994). However, Bercovitch (1987) found that male olive baboons did not seem to be able to differentiate between conceptive and non-conceptive cycles.

Behaviour and Paternity Outcome

Mate-guarding was typically a strategy of prime-aged, top-ranking males, as in other primate species (e.g. Berard et al. 1994; Huffman 1992; Small 1990). The percentage of mate-guarding by a

male correlated strongly with the percentage of offspring sired, and an alpha male was more likely to sire when he mate-guarded than when he did not. However, as is generally the case (Hughes 1998) the relationship between behaviour and paternity outcome was not perfect: males that were too young to mate-guard still sired, not all sires mate-guarded, and even if the alpha male mate-guarded a female during her entire peri-ovulatory period, he did not necessarily sire the resulting offspring. These discrepancies confirm that females may mate with multiple males per receptive period, indicate the success of sneaky, opportunistic mating tactics by non-alpha males, and mean that mate-guarding consistently overestimated the reproductive output of alpha males.

The Priority-of-Access Model

A specific goal of this study was to examine the predictions of the priority-of-access model for mate-guarding and paternity outcome. The fit of the observed data was generally good for both mate-guarding and for paternity. However, in both cases, the alpha male was more successful than predicted, second- and third-ranking males were less so, and males that were not predicted to mate-guard or sire, because they ranked too low, did both. Paternity deviation from the priority-of-access model was not similarly influenced by the number of females, nor indeed by any of the variables tested. Although paternity patterns will not necessarily be influenced by the same variables as mate-guarding, the lack of any explanatory variables is likely to also relate to the inaccuracy of generating paternity predictions for the small numbers of offspring born in any one year based on the degree to which six-day peri-ovulatory periods overlap.

Alpha male mandrills were more able to monopolise access to receptive females than alpha male yellow baboons are. This difference is unlikely to be due differences in group size: the group sizes in the study of yellow baboons (2-14 adult males, 8-24 females) are comparable to those for the mandrills studied here. Although our study groups included fewer adult males (maximum 8), older adolescent male mandrills can out-rank older adult males (Setchell 2003), the criterion used for adulthood in baboons, increasing the maximum number of rival male mandrills to 11. Instead, the major difference between these two species appears to be the absence of male-male coalitions in mandrills (Setchell & Wickings 2005), as in chacma baboons (Bulger 1993). According to a model

developed recently by Pandit & van Schaik (2003) coalitions are feasible only where contest among males is not too strong, and where costs of coalition formation are moderate. It appears that male contest is simply too strong in mandrills for coalitions to be profitable, and they thus do not occur. Moreover, in a dense habitat sneaky mating is likely to represent a better strategy than the formation of noisy and conspicuous coalitions against mate guarding males, because the latter could attract further males that may profit from the situation.

Mate-guarding patterns in mandrills were also more similar to those reported for chacma baboons than for yellow baboons. Although conditions in the colony preclude detailed observation of mate-guarding, mate-guarding pairs never changed from the morning to the afternoon observation period, implying that turnover was rare. Where mate-guarding males changed overnight this appeared to be due to a lack of interest by the alpha male, rather than to challenge by a non-alpha male. Turnover of mate-guarding males is similarly rare in chacma baboons (Bulger 1993), but common in yellow baboons (Noë & Sluijter 1990). Correspondingly, the length of continuous mate-guarding (mean 5 days) in mandrills was more similar to the length of consortships in chacmas (Bulger 1993; Weingrill et al. 2000) than in yellow baboons (Smuts 1985; Sluijter 1990). Finally, the majority of female receptive cycles were only mate-guarded by one male in mandrills, as in chacmas (68% of all cycles, 76% of conceptive cycles, Bulger 1993) whereas in yellow baboons many males mate-guard for short periods of time (Hausfater 1975).

Factors Influencing the Monopoly of Receptive Females by Alpha Males

Our sample includes relatively few group years, meaning that we were able only to identify major influences on the ability of alpha male to monopolise females. However, in addition to confirming dominance-based priority-of-access to receptive females, we found that reproductive monopoly by the alpha male was negatively related to the number of males present (adult males for mate-guarding monopoly, and all reproductive males for paternity). This reflects a common primate pattern: decreased monopoly as the number of competing males increases has been shown both among and within populations, although it is difficult to disentangle the relative influence of increased numbers of males and females, which are highly correlated (van Noordwijk & van Schaik 2004). Rival

males may be resident in a group or a combination of resident and extra-group males. For example, the chance of an individual extra-group male Japanese macaque mating increases when there are many such males, and when a high number of simultaneously receptive females is available relative to the number of resident males (Takahashi 2001). Similarly, multi-male influxes in blue monkeys (*Cercopithecus mitis*), where multiple extra-group males invade a uni-male, multi-female group during the mating season, are rare where population densities, and thus numbers of extra-group males, are low (Cords 2000), and multi-male mating in patas monkeys (*Erythrocebus patas*) is related to the availability of extra-group males (Carlson & Isbell 2001). This may be relevant to mandrills, as adult males of this species vary greatly in group association in semi-captivity (Setchell & Dixson 2001a; Wickings & Dixson 1992), and both group-associated and solitary males occur in the wild (Rogers et al. 1996).

Although the number of males influenced alpha male monopolisation of receptive females, it was not a significant influence on deviation from the predictions of the priority-of-access model. This implies that an alpha male is able to cope with increasing numbers of rivals, as long as female peri-ovulatory periods do not overlap. However, as group size increases, both the number of simultaneously peri-ovulatory females and the number of males increase. Similarly, in a study of chacma baboons Bulger (1993) found no difference between small (3-5 males) and large (7-11 males) male cohorts either in alpha male consortship success nor when the presence of simultaneously receptive females was taken into account. Weingrill et al (2003) also found that numbers of males and females in chacma baboon groups were poorly related to the consortship success of alpha males. In this study of a population where female inter-birth intervals are particularly long, the authors suggest that consortship success of alpha males is primarily determined by the number of receptive days a male encountered (Weingrill et al. 2003).

In this provisioned situation, alpha males mate-guarded more than expected as the number of females increased – the opposite of the pattern expected if males experienced mate-guarding fatigue (e.g. Weingrill et al. 2003). This may be partly due to males being less constrained by food availability than they would be in the wild, and thus able to mate-guard for long periods. However, mate-guarding males clearly adapt their activities to their female partners, their feeding is often interrupted

(unpublished observations), and there is some evidence that alpha males do lose "fattedness" across the mating season (Setchell & Dixson 2001b), as reported for rhesus macaques (Bercovitch 1997; Bercovitch & Nürnberg 1996). Competition costs of mate-guarding also appear to be high, as mate-guarding males appear highly stressed by the near constant close presence of subordinate rival males, frequently chase and wrestle with rivals, and may receive serious wounds (unpublished observations).

We found no influence of the duration of alpha male tenure on mate-guarding or paternity by alpha males. Studies of other species have shown that newly dominant males may initially show poor mating success (Hausfater 1975; Noë & Sluijter 1990; Smuts 1985). This finding has been related to the need to establish both social relationships with females (Smuts 1985; Strum 1982) and rank relationships with other males (Alberts et al. 2003). Such males also tend to be (but are not always) newly immigrant males, and a partial explanation for the lack of such an effect in these mandrills may therefore be that all animals were familiar with one another in this closed colony. Conversely, male mating success and paternity decrease as male tenure increases in some species, a finding that has been explained by female choice against mating with males that were dominant when the female was immature, and are thus potentially the female's own father (see refs in Berard 1999). Again, this was not observed in the mandrill colony, although females did not have the possibility of mating with novel (immigrant) males.

Wild Mandrills

Although several features of the semi-free-ranging colony may limit extrapolation of our results to wild mandrills (provisioning, a lack of transfer opportunities for males into and out of groups) we can make some predictions about patterns of male reproductive skew in wild mandrills. Wild groups of mandrills range in size from 15 to hundreds of individuals (Abernethy et al. 2002; Hoshino et al. 1984; Rogers et al. 1996), and even small groups may contain more than one adult male (Hoshino et al. 1984). In smaller groups a single dominant male may be able to mate-guard peri-ovulatory females, and sire the majority of offspring, as in smaller group-sizes during this study. However, the largest reported wild groups (mean group size 620) contain a mean of 182 adult females, with 1-17 adult

males (mean 7) and 56 males estimated as >5 yr (Abernethy et al. 2002). Even if each individual female reproduces on average only once every two years in the wild, approximately 90 females may be expected to cycle during the same mating season. Female peri-ovulatory cycles are therefore likely to overlap extensively, and dominant males will be unable to control access to all peri-ovulatory females. Moreover, the dense forest habitat has many visual obstructions, facilitating sneak copulations with non-mate-guarding males, while the costs associated with mate-guarding will be far higher in the wild than in our provisioned colony, decreasing both the potential for monopolisation, and likely the tenure of dominant males, due to loss of condition. Large group sizes also mean that male dominance ranks are likely to be unstable. Indeed, it seems possible that at least some males may move into and out of the same or different social groups, depending on the presence of receptive females and other males, and their own condition and nutritional requirements (cf. African buffalo, Prins 1996), as numbers of males appear to fluctuate over time (Abernethy et al. 2002). Together, these factors are likely to decrease the monopolisation of receptive females by individual males in the wild by comparison with this captive situation. Tests of these predictions will require studies of wild populations at levels that are currently not possible.

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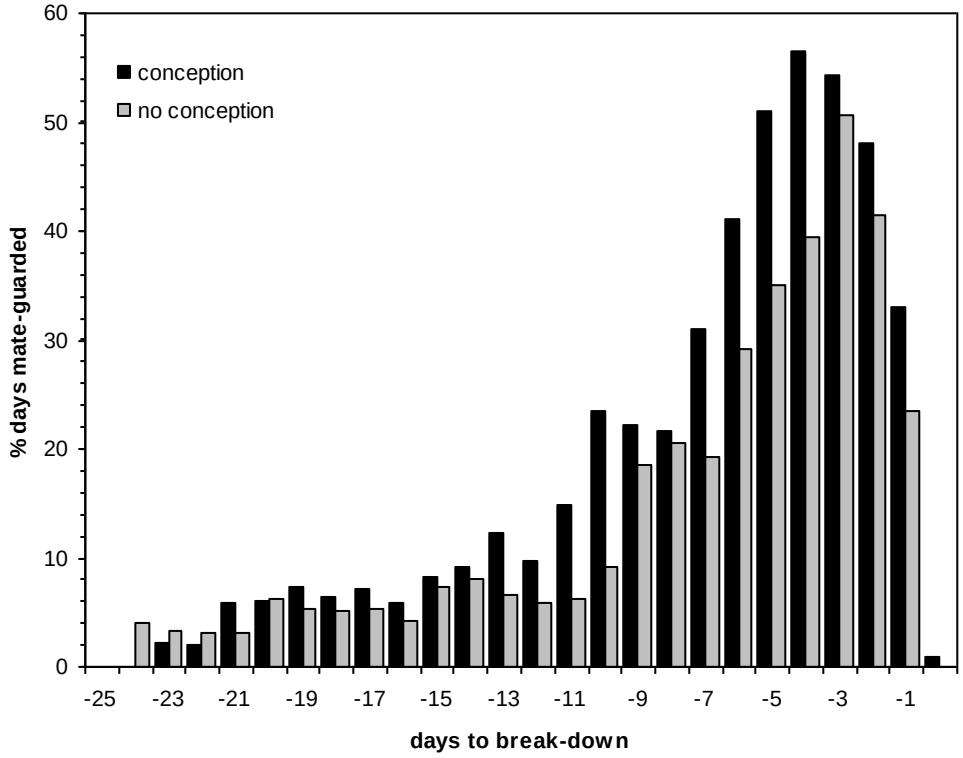
Fig. 1 Percentage of conceptive and non-conceptive cycles on which mate-guarding occurred vs. number of days to swelling break-down (above) and days since onset of sexual swelling (below). Sample size varies from 27-106 for conceptive cycle days (mean 72±4), and from 18-92 for non-conceptive cycle days (mean 53±4).



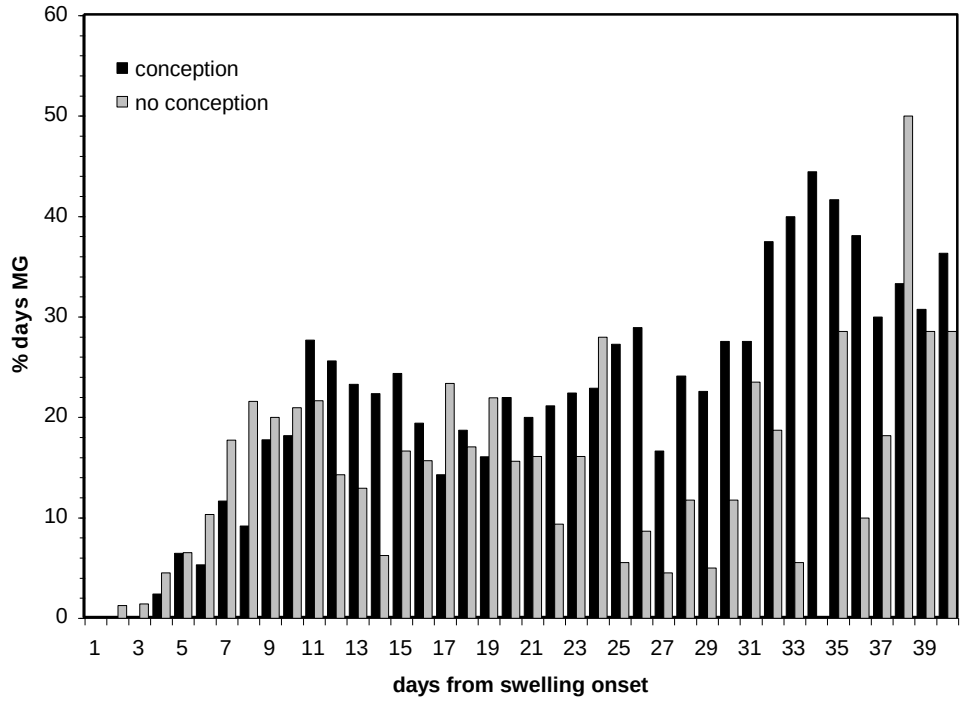


Fig. 2 Number of males that mate-guarded females during each conceptive and non-conceptive cycle, and during each conceptive and non-conceptive peri-ovulatory period.

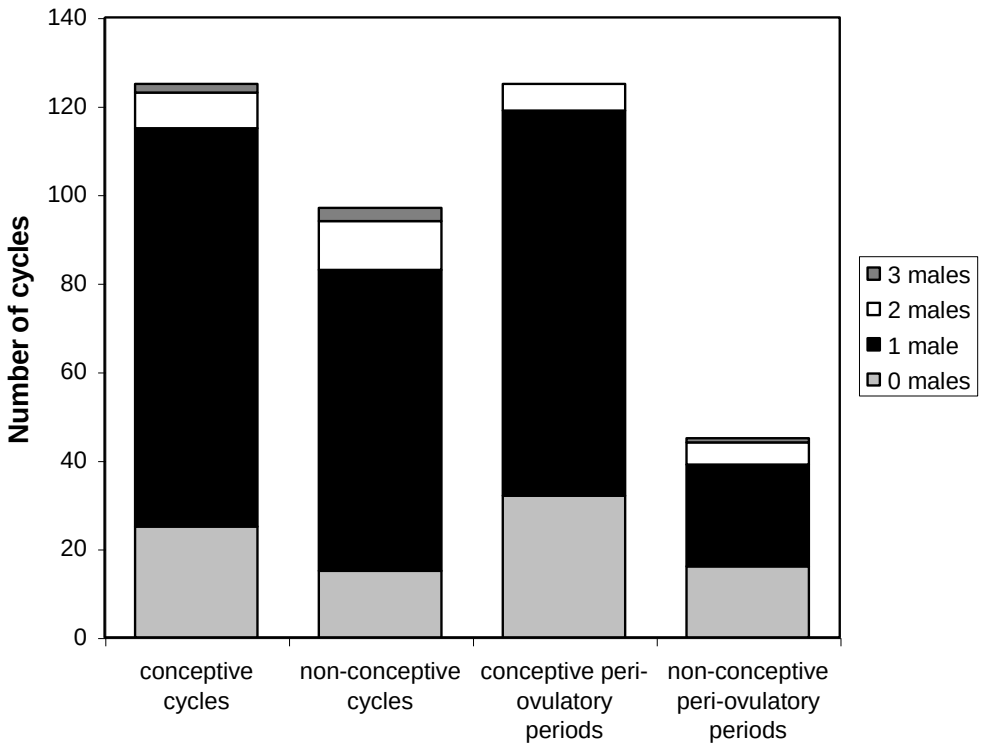


Fig. 3. Number of peri-ovulatory days mate-guarded by males of each rank. Predicted values calculated from the distribution of female peri-ovulatory periods, using the priority-of-access model.

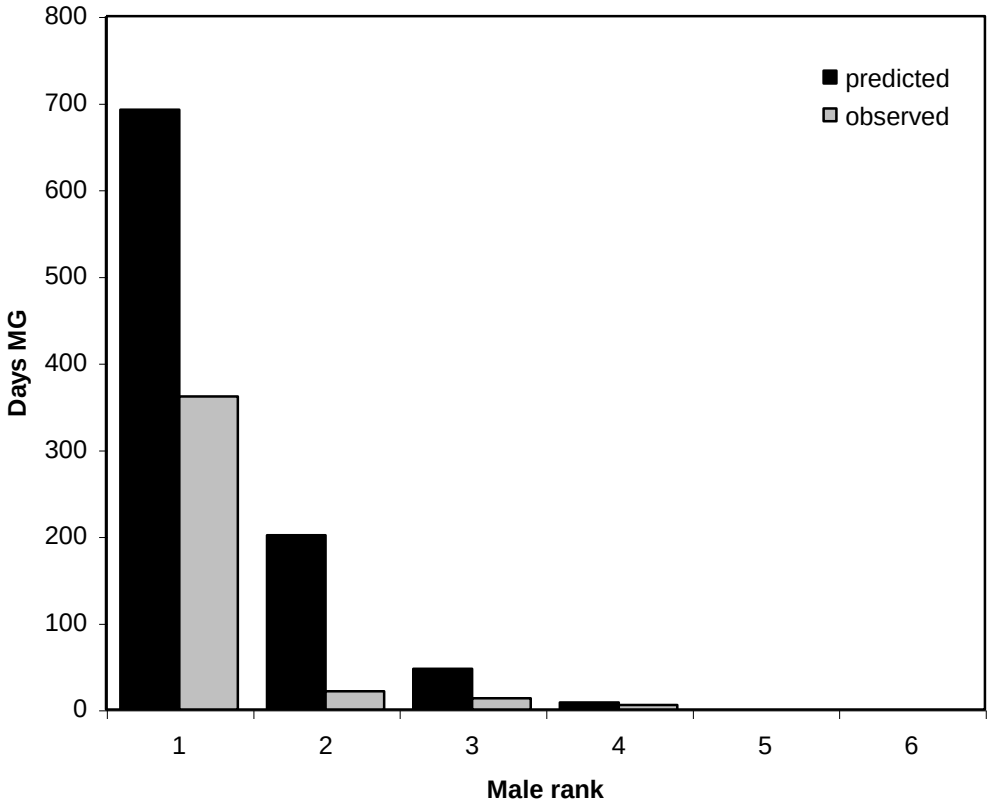


Fig. 4. Number of sexually swollen and peri-ovulatory females available on any one day during the study period.

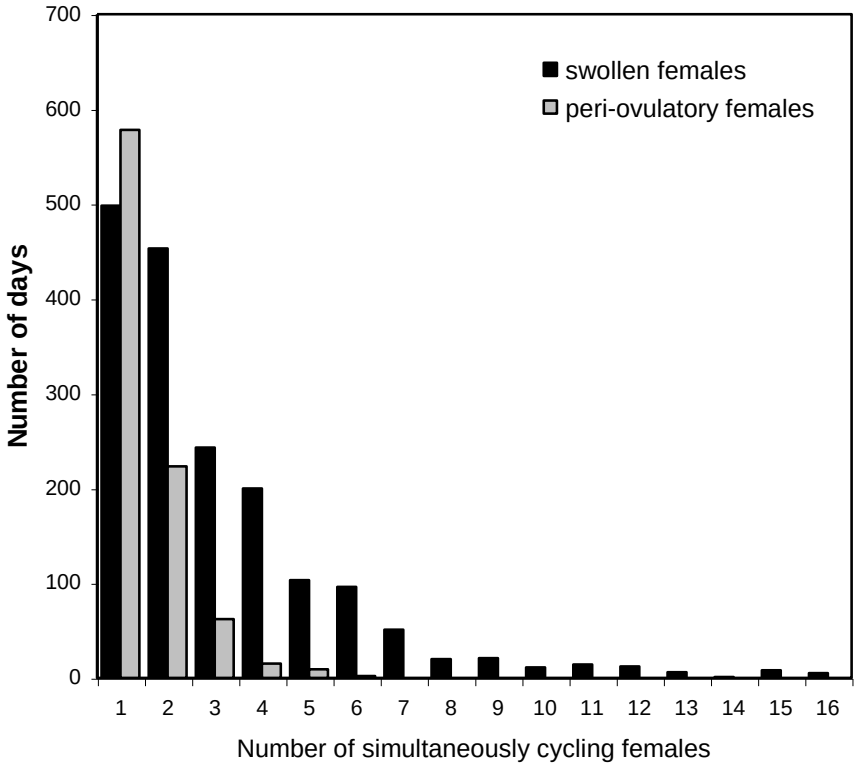


Fig. 5. Number of offspring sired by males of each rank. Predicted values calculated from the distribution of female peri-ovulatory periods, using the priority-of-access model.

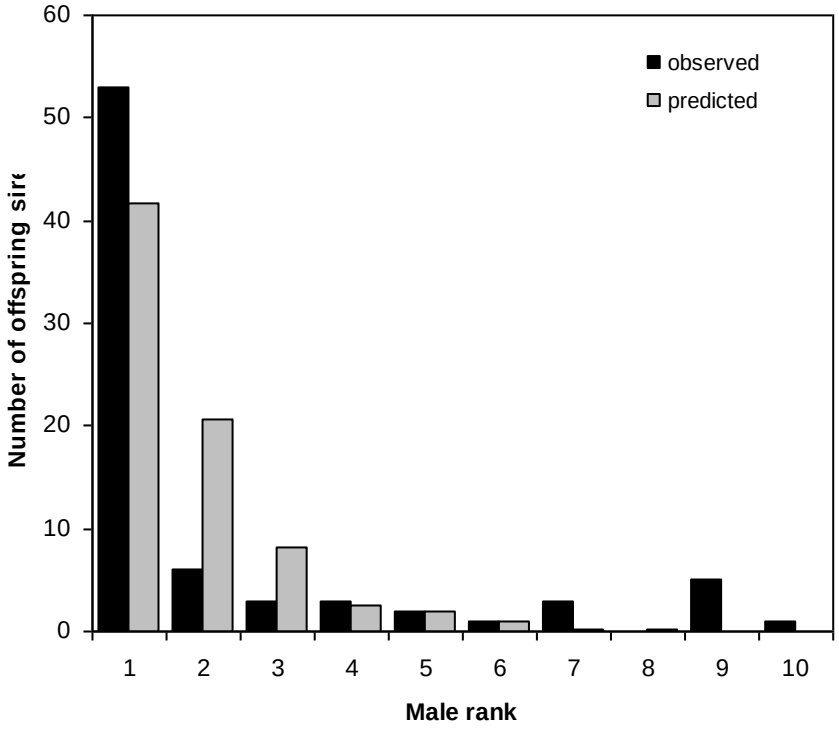


Fig. 6 Number of conceptive peri-ovulatory days mate-guarded vs. number of offspring sired for the period for which both behavioural and paternity data were available. Small symbols indicate single data points, medium symbols indicate two data points, and large symbols three data points.

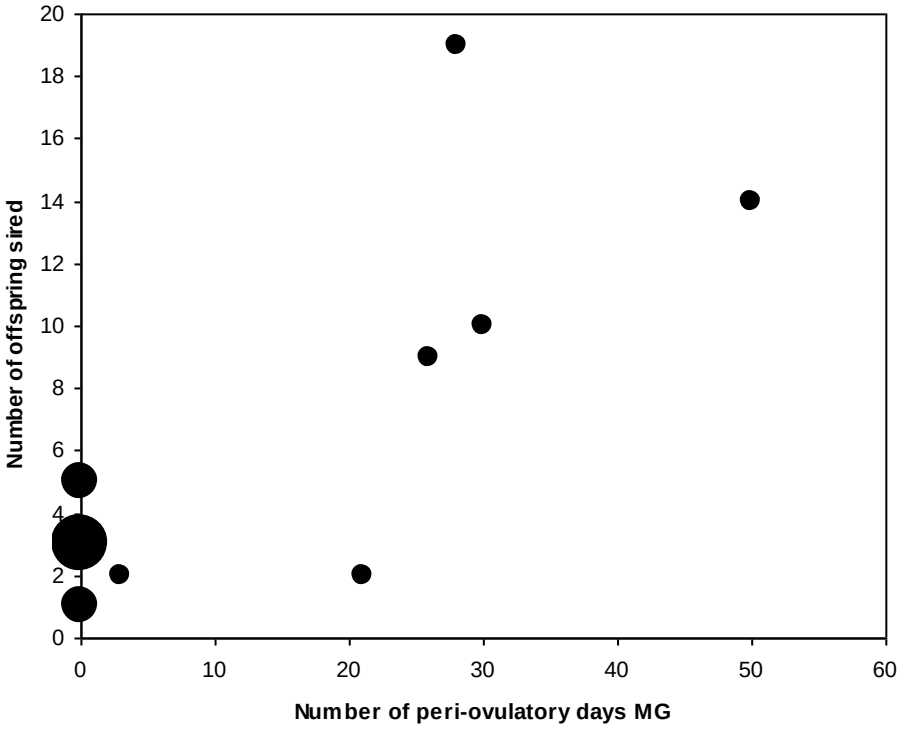


Table 1: Composition of the study groups, with numbers of cycles, conceptions and known paternities

Year	Adult males [1]	Older adolescent males [2]	Younger adolescent males [3]	Reproductive females [4]	Juveniles and infants	Total group size	Number of cycles	Number of conceptions	Number of known paternities
Enclosure 1									
1996	1	4	6	13	12	36	18	12	11
1997	3	5	6	13	20	47	15	9	5
1998	5	4	8	19	29	65	14	13	11
2000	8	1	12	22	24	69	18	18	15
2001	6	3	12	27	28	81	19	11	9
2002	8	3	14	31	48	104	25	10	0
2003	5	2	7	19	36	69	18	8	0
Enclosure 2									
1996	5	0	4	6	6	21	9	7	6
1997	4	2	2	6	14	28	2	1	1
1998	4	2	3	10	11	30	5	7	7
2000	4	0	5	13	14	36	8	9	6
2001	4	0	6	13	21	44	5	4	3
2002	4	2	5	15	26	52	14	11	0
2003	3	3	6	16	14	42	4	4	0

[1] Adult males: males aged >10.0 yr; [2] Older adolescent males: males aged 8.0 to 10.0 yr; [3] Younger adolescent males: males aged 3.8 to 8.0 yr; [4] based on ages at 01 May, the approximate beginning of the mating period. Reproductive females: females undergoing reproductive cycles

Table 2: Results of multiple regressions investigating the influence of various predictor variables on monopoly of mate-guarding and paternity by alpha males

Dependent variable	R^2_{adj}	Mean square		F	p	Predictor variables	ß	t	p
		regression (df)	residual (df)						
Alpha male monopoly of MG	0.403	353.92 (1)	427.31 (11)	9.111	0.012	# adult males	-0.673	-3.018	**0.012**
						# reproductive males	0.143	0.417	0.686
						# receptive females	0.069	0.239	0.816
						Alpha male tenure	-0.213	-0.826	0.428
Deviation of MG from PoA	0.271	0.098 (1)	0.197 (11)	5.470	0.039	# adult males	-0.411	-1.405	0.190
						# reproductive males	0.090	0.213	0.835
						# receptive females	0.576	2.340	**0.039**
						Alpha male tenure	-0.148	-0.535	0.604
Alpha male monopoly of paternity	0.406	2227.525 (1)	344.354 (8)	6.469	0.038	# adult males	0.106	0.041	0.969
						# reproductive males	-0.693	-2.543	**0.038**
						# receptive females	0.318	0.648	0.541
						Alpha male tenure	-0.247	-0.727	0.494
Number of males siring	0.674	13.416 (1)	0.685 (8)	19.573	0.002	# adult males	-0.125	-0.473	0.650
						# reproductive males	0.843	4.424	**0.002**
						# receptive females	-0.125	-0.473	0.650
						Alpha male tenure	-0.203	-0.909	0.394
Discrepancy MG and paternity	0.546	1536.542 (1)	1299.822 (8)	11.836	0.009	# adult males	-0.471	-1.808	0.114
						# reproductive males	0.772	3.440	**0.009**
						# receptive females	-0.194	-0.489	0.640
						Alpha male tenure	-0.204	-0.763	0.470

PoA: Priority-of-access model; MG: mate-guarding; significant p-values are highlighted in bold for predictor variables